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Shrinking the Janzen-Connell Doughnut: Consequences of an Invasive Multiplier (Microstegium vimineum) on the Mid-canopy in a Mixed Pine-Oak Forest

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SHRINKING THE JANZEN-CONNELL DOUGHNUT: CONSEQUENCES OF AN INVASIVE MULTIPLIER (*MICROSTEGIUM VIMINEUM*) ON THE MID-CANOPY IN A MIXED PINE-OAK FOREST

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

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SHRINKING THE JANZEN-CONNELL DOUGHNUT: CONSEQUENCES OF AN INVASIVE MULTIPLIER (*MICROSTEGIUM VIMINEUM*) ON THE MID-CANOPY IN A MIXED PINE-OAK FOREST

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Introduction of invasive species can alter seed fate predictions made by the Janzen-Connell Escape Hypothesis (JCEH). The JCEH states that there is a suitable region around a plant that is ideal for seed germination, growth, and recruitment. Seeds dispersed too close to the maternal plant are subject to competition from the maternal individual and perhaps density-dependent predation, whereas seeds dispersed further away may end up in suboptimal habitats. Invasive species may change the amount of these suitable habitats for native plants by creating unsuitable light environments and as a result, may influence the

size of the ideal recruitment zone surrounding a parent plant. This study examines the extent to which the invasive grass species, *Microstegium vimineum*, influences recruitment of the understory tree, *Cornus florida*. In general, *M. vimineum* was found to reduce both germination and early seedling success and may have significant consequences for future forest structure.

Introduction

The Janzen-Connell escape hypothesis (JCEH) predicts the distribution of tree recruitment in forests resulting from the interaction of two different processes influencing offspring survival. First, most plants disperse seeds in a leptokurtic fashion away from the maternal individual such that the majority of seeds fall near the parent plant and few are dispersed great distances (Cain *et al.* 2000, Clark *et al.* 1999; Okubo and Levin 1989). For species that inhabit variable environments, a leptokurtic dispersal means that offspring that move long distances have an increased probability of landing in either sub-optimal or ill-adapted habitats. For example, Sork *et al.* (1993) showed that seedlings from the canopy tree species, *Quercus rubra*, exhibited fine-scale adaptation for resistance to herbivores based upon the slope aspect of the maternal individual. Canopy trees on south-facing slopes had offspring that were more able to resist phytophagous insects on south-facing slopes than if the same offspring were planted on north-facing slopes, and likewise for the reciprocal planting. These results suggest that local adaptation and variability in habitat suitability, even for a wind-dispersed canopy tree, may be on the order of meters rather than kilometers. Furthermore, it would be expected that selection would favor limited dispersal in this system as seeds dispersed great distance from the maternal individual may land in habitats with different aspect and corresponding guild of phytophagous insects than the

maternal individual's habitat. For the purposes of the JCEH, habitat heterogeneity and selection are expected to favor limited dispersal of propagules.

In opposition to the dispersal process, the second component of the JCEH focuses on seedling survival as a function of the proximity to the maternal individual. Large seed crops may reduce the likelihood of survival due to density dependent responses of seed-predators beneath the parent canopy (e.g., Kwit *et al.* 2004, Janzen 1970). Indeed, density-dependent seed predation is such an important process that it is considered one of the reasons temperate trees exhibit masting behavior (e.g., Ballardie and Whelan 1986; Sork 1993). As a result, individual propagules that are dispersed in close proximity with each other may be selected against due to predation pressures. In addition to predation, dispersal under the maternal individual may also negatively influence survival because the seedling must compete for limited resources with the maternal individual, which is already on site and established. As a result, predation and competition are expected to result in selection for increased dispersal distance away from the parent plant. Combining both selection for habitat similarity with increased dispersal, the JCEH predicts an optimum dispersal distance around the maternal individual. This optimum ring, or "doughnut," around the maternal individual depends upon the relative strengths of these opposing selective forces (e.g., Figure 1).

Introduction of invasive species can modify the predictions made by the JCEH if the presence of the invading species changes existing habitats in such a manner as to make them less suitable for native tree recruitment and growth (Taverna *et al.* 2005, Claridge and Franklin 2002, White and Schwarz 1998, Gilliam 2007). Changes in habitat suitability

will result in a reduction in the size of the "doughnut," or ideal recruitment zone surrounding a maternal tree. Given the importance of the environment that the seed is dispersed into for overall germination and survival, quantifying how invasive species modify habitat suitability becomes paramount in understanding how invasion influences recruitment and by extension subsequent forest structure. If the invasive species does not make appreciable changes to local environment suitability for tree recruitment, but only displaces native species, then it is not expected to modify recruitment in a significant manner. However, if the invading species create light and nutrient conditions that are differentially suitable for tree recruitment, then we expect to see dramatic changes that can result in subsequent large-scale modification in overall community structure through time (e.g., Dehlin *et al.* 2008, Oswalt *et al.* 2007).

Changing the light environment in such a way as to prevent germination of other species is a common strategy used by several invasive species. For example, *Acer platanoides*, an upper canopy tree invading forests in the northeastern United States, creates an environment beneath its canopy that has less than five percent of the amount of light found beneath native canopies. Reinhardt *et al.* (2006) found that this reduced light environment decreased the survival of several native tree seedlings by 28-55% but had no effect on the *A. platanoides* seedlings. These results suggest that the low light environment produced beneath *A. platanoides* leads to higher rates of native plant mortality while aiding in *A. platanoides'* own success (Reinhardt *et al.* 2006). As *A. plantanoides* continues to invade, subsequent recruitment of native species will be

adversely influenced, and over time, forest structure will change as *A. plantanoides* increases in relative importance.

Invasive species themselves are not immune to modifications of the light environments, and light may play a role in shaping how invasives move into a community (Cole and Weltzin 2005, Holly and Ervin 2007, Hotchkiss *et al.* 2008). For example, Knight *et al.* (2008) found that successful seedling recruitment of *Prunus serotina*, a timber tree that is invasive in Europe, was dependent on the light environment created by the upper canopy. Fewer seedlings were able to thrive under canopies that had a higher percent cover, and thus reduced light (Knight *et al.* 2008). Clearly, tolerance to a wide variety of light conditions should be proportional to invasability (Standish 2002, Cole and Weltzin 2005, Hotchkiss *et al.* 2008).

A recent addition to the list of invasive species in the Eastern United States is the grass *Microstegium vimineum* (Poaceae), commonly referred to as Chinese Packing Grass. *Microstegium vimineum* is an exotic invasive grass that is prevalent in a variety of habitats, including open moist fields, roadsides, forest edges and deep understory sites. This species was first introduced to the US in 1919 and has subsequently spread to all states south of Connecticut and east of the Mississippi River (Rhoads and Block 2002). This species is able to rapidly invade disturbed understory habitats and crowds out most of the native vegetation, becoming the dominant understory plant species in disturbed areas (University of Maine Cooperative Extension 2004, Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997). Closed-canopy areas of deciduous forests can easily support dense stands of *M. vimineum*. However, the presence of a well defined

secondary canopy seems to reduce light to a level where *M. vimineum* may not be able to invade. For example, Cole and Weltzin (2005) found conspicuous gaps of *M. vimineum* beneath the mid-canopy tree *Asimina triloba*. The light environment beneath the full canopy and *A. triloba* individuals was reduced to approximately one percent of full ambient sunlight (Cole and Weltzin 2005), a level sufficient to prevent invasion by the grass. Greenhouse experiments confirmed that light environments with less than 8% of full ambient sunlight would be sufficient to inhibit the spread of *M. vimineum* (Cole and Weltzin 2005). These results suggest that *A. triloba* is able to control *M. vimineum*'s invasive ability by limiting the amount of available light beneath its canopy as long as *A. triloba* can remain on-site.

While an adult *A. triloba* canopy was able to control the spread of *M. vimineum*, this invasive may still pose a threat to other life stages of trees. Oswalt *et al.* (2004) studied the effect of *M. vimineum* and herbivory on *Quercus rubra* seedling success. They found that herbaceous growth (*M. vimineum* was the most prominent herbaceous plant in the test plots) seemed to protect seedlings from herbivory as it is so dense it that most insects do not find it a suitable habitat. However, they also noted that test plots with the largest populations of *M. vimineum* experienced the lowest amount of seedling growth. These results imply that *M. vimineum* has characteristics that not only allow it to invade new areas but also help it to replace native flora.

This study investigates the effect of the invasive grass, *Micostegium vimineum* on the recruitment of mid-canopy trees in a deciduous forest, as well as possible implications *M. vimineum* invasion may have on future canopy recruitment. In the Piedmont region of

Virginia, *Cornus florida* L. (Cornaceae) and *Cercis canadensis L.* (Fabaceae) are two of the main mid-canopy species and are used in this study to investigate the range of mid-canopy seed dispersal and the relationship(s) between recruitment and survival of these mid-canopy species and *M. vimineum*. First, seed dispersal distances will be quantified by a multi-year seed-trap sampling scheme to quantify the potential distances that seeds may be dispersed away from the maternal individual. Here only *C. florida* will be used as it occurs with sufficient density for this kind of analysis at the study site. The dispersal distributions will quantify the extent to which seeds can be dispersed away from individual trees. Next, *C. florida* will be used to determine if its canopy is sufficient to block enough light such that it prevents the spread of *M. vimineum* similar to what Cole and Weltzin (2005) found for *Asimina triloba.* This allows the quantification of light conditions within stands that have a well developed secondary canopy and will aid in understanding how *M. vimineum* may be prevented from complete invasion. Finally, seeds from both tree species will be used to test the influence of *M. vimineum* on seedling germination and survival. A set of common garden plots for each species with and without the presence of *M. vimineum* will be used to monitor early recruitment success. The extent to which *M. vimineum* influences recruitment will aid in determining how future canopy structure may be changed by this grass and gives support for the tightening of the Janzen-Connell "doughnut" around the maternal individuals. The results of this study will help inform future management practices on the importance of the mid-canopy layer of deciduous forests with respect to aiding in the control of invasive species and maintaining biodiversity within forest systems.

Methods

Study Site and Species:

This experiment was conducted at the Inger and Walter Rice Center, a research station operated by Virginia Commonwealth University and located in Charles City, Virginia (N: 37.339, S:77.206; Figures 2 and 3). This research station consists of 138.4 ha of second growth piedmont forest along the north bank of the James River (VCU 2008). The vegetation at the Rice Center is characterized as southern pine-oak forest. Canopy species include (in decreasing order of relative importance): *Pinus taeda*, *Quercus ru*bra, *Q.velutina*, *Q. alba*, *Acer rubrum*, *Carya floridana*, and *Liriodendron tulipifera*. The mid-canopy is composed of *Cornus florida* and *Cercis canadensis*, two mid-canopy plants of interest in this study, as well as *Ilex opaca*, and to a lesser degree *Sasafrass albidum*. The herbaceous layer is highly variable and can include *Podophyllum peltatum*, *Dryopteris marginalis*, *Botrychium virginianum*, and *Polystichum acrostichoides*, *Dicentra cucullaria*, and *D. canadensis*.

The Rice Center has several moderately sized "blow down" areas where, in 2003, Hurricane Isabelle uprooted many trees, creating disturbed areas. Since then, the invasive grass *Microstegium vimineum* has grown rampant in these disturbed areas, covering most if not all of the ground there. *Microstegium vimineum* is an annual, invasive, generally shade-

tolerant C_4 grass that can compete with and/or replace native ground layer flora in three to five years. This grass does extremely well in areas where there has been disturbance such as "blow down" areas (Oswalt and Oswalt 2007). Seeds are dispersed through animal-, water- or gravity-mediated seed dispersal and create a persistent, one to three year seed bank (Tennessee Exotic Pest Plant Council and Great Smoky Mountains National Park 1997, Gibson *et al.* 2002, Barden 1987). The mating system of *M. vimineum* is particularly well suited for an invasive as it can easily self and outcross to create seeds, the relative rates at which have been shown to be influenced by local environmental conditions (Cheplick 2006). The success of *M. vimineum* as an invasive plant can be attributed to having traits of both shade tolerant plants and plants that occur in high light environments (Horton and Neufeld 1998) and its ability to produce a large seed crop in varying environments (Gibson *et al.* 2002, Claridge and Franklin 2002). Its ability to adapt in different environments makes it difficult to quantify a single growth rate for the plant. In one study, *M. vimineuem* increased its overall cover by 11% over two years (Barden 1987), while in another, it increased with an average linear spread of 1.66 m in disturbed areas and 0.37 m in non-disturbed areas (Oswalt *et al.* 2007). *M. vimineum* is proving to be an enigma for scientists because it can grow and succeed in a wide range of habitats. This plasticity makes *M. vimineum* a difficult weed to prevent its invasion and/or control the spread of existing patches.

Cornus florida, or the flowering dogwood, is a common mid-canopy tree that has a large eastern North American distribution. It can grow to a height of 6-11 m and has an average canopy spread of 7-9 m, approximately the same size as *A. triloba* (mentioned

above; Gilman and Watson 1993). *Cornus florida* is insect-pollinated by a wide variety of early season pollinators, and is predominantly an outcrossing species producing less than three percent selfed progeny during natural pollination (Sork *et al.* 2005; Gardiakos and Dyer, In Prep). It flowers from late March through April, producing one-seeded, oblong/ellipsoid red drupes 8-14 mm long on an infructescence. Adult trees, on average, produce 185 kg of fruit per square meter of a tree's basal area (USDA Forest Service Silvics of North America 1990). The fleshy fruits are mainly dispersed by gravity or by songbirds such as hermits, olive-backs, gray-checked thrushes, and northern cardinals (Kwit et al. 2004, USDA Forest Service Silvics of North America 1990).

Cercis canadensis, commonly known as the redbud, is a co-occuring mid-canopy, deciduous tree found throughout the eastern United States. It is similar in height and canopy spread to *C. florida* and *A. triloba* (Gilman and Watson 1993). *Cercis canadensis* produces leguminous fruits that are flat, reddish-brown pods about 1.3 cm wide and 5 to 10 cm long. Each fruit contains 4 to 10 brown, hard, compressed bean-like seeds, each about 6 mm long. The fruits remain on the tree until after leaf fall, though some persist throughout winter. The opening of fruit sutures or decay of the fruit wall releases seeds during the fall and winter so wind, gravity and animals can then disperse them. Seeds that fall to the ground can remain dormant for several years (Banner and Stein 2008).

Quantifying Seed Dispersal in *Cornus florida* L.:

Seed dispersal distance for *C. florida* was determined by deploying three arrays of seed traps. The first array consisted of 14 1.0 x 0.5 m seed traps distributed in two

orthogonal linear arrays radiating away from a single maternal individual that demonstrated consistent high seed crops over several years (personal observation). Seven traps were deployed along each leg of the arrays at 1 m intervals. This array was focused on a single isolated tree such that all collected seeds will be presumed to come from a single source. It is possible that some of the seeds being dispersed into this seed array could originate form maternal trees other than the target one, however, these would represent rare long-distance dispersal events.

The second and third trap arrays each consisted of seven similar sized seed traps distributed away from a focal tree located in a glade of fruiting *C. florida* indivduals. The second array extended from a tree at the edge of a glade 9 m away from the glade. The third array started from a *C. florida* specimen located in the middle of the glade and extended 9 m opposite of the second array. These last two arrays focused on dispersal from potentially several individuals in a glade outwards into the forest.

Seeds were collected bi-weekly from the seed traps and sorted into three distinct groups; fully pulped, partially eaten, and depulped. These designations were chosen because they may be slightly predictive of the dispersal type. Seeds that were fully depulped or partially eaten had the potential to be dispersed by a bird from a tree other than at the trapping location. Conversely, fully pulped seeds were considered to be more likely to have originated from the tree closest to the trap. To account for variation in canopy size, which may influence the estimated dispersal distances, the average canopy radius was measured for each focal tree and all estimates reported below are reported as the distance away from the edge of the canopy rather than the distance from the stem (Blozan 2008).

After sorting, all seeds were cold stratified for 120 days at 5ºC. Seeds were collected in the fall of 2006 and 2007. Kurtosis, or the skew in the dispersal function, was estimated for each type of seed distribution at each of the trees using SAS (version 8.2). Confidence intervals for the dispersal distance observed in each array was determined by random permutation, with replacement, of the empirical data.

Light Environments

A well developed secondary canopy has the potential to obstruct enough light such that *M. vimineum* cannot persist (Cole and Weltzin 2005, Gibson *et al.* 2002). How *C. florida* (the dominant mid-canopy tree species at the Rice Center) and *M. vimineum* (the invasive) modify the light environment beneath their respective canopies was determined using a LI-COR 1400 data logger with LI-COR LI-190 Quantum sensors to sample under each species. Sensors were positioned in three locations. One was beneath both an upper canopy and a *C. florida* sub-canopy. Another was beneath both an upper canopy and a patch of *M. vimineum* but without the presence of a sub-canopy. A third sensor was located in a nearby open field to provide a point of reference for the amount of light available with no canopy covering (the sun icon in figure 3 shows where this field was located). The amount of light in $\mu Moles/m^2/second^{-1}$ was recorded once every fifteen minutes from 06:15 to 21:00 (approximately an hour before and after sun-up and sun-down) the week of October 14th in 2007. This week was mostly sunny with some clouds and the seasonal leaf fall had not yet occurred. Measurements were collapsed across time to provide estimates of light in $\mu Moles/m^2/day^{-1}$.

The effect of canopy presence on light was determined by a one-way ANOVA with canopy (open field, under *C. florida*, or under *M. vimineum*) as the main treatment effect (SAS version 8.2, Ott and Longnecker 2001). A Tukey's post-hoc test was used to quantify the magnitude and ordering of treatment means (SAS version 8.2) following the design from Ott and Longnecker (2001).

Asimina triloba, a mid-canopy tree, limited the spread of *M. vimineum* beneath its canopy by creating a light environment unsuitable for its growth (Cole and Weltzin 2005). *Cornus florida* (a similarly canopied mid-level tree) has the potential to create a comparable light environment beneath its canopy, thus allowing it to also act as a control mechanism for *M. vimineum* invasion. A census of *M. vimineum* in 0.3x0.3 m quadrants under and outside the canopies of *C. florida* individuals was taken. Each sampling location was haphazardly placed in six locations beneath two different *C. florida* canopies. The same method was used to sample from six locations located outside the canopy of *C. florida.* The number of *M. vimineum* specimens was counted within each square. A *t*-test was performed to determine if there was a significant difference between the mean number of *M. vimineum* specimens located beneath a *C. florida* canopy and located just outside of a *C. florida* canopy (SAS version 8.2, Ott and Longnecker 2001).

Recruitment

The consequences of *M. vimineum* on secondary canopy recruitment were assayed by deploying arrays of seeds in test plots. Due to the lack of apparent natural recruitment in the presence of *M. vimineum*, and the variable germination rates in *C. florida* and *C.*

canadnesis, a two-factor experiment was performed. *Cornus florida* fruits collected in the fall of 2005 on site were used in these plantings. These seeds were processed and cold stratified as explained above. Due to the low number of *C. canadensis* individuals at the Rice Center from which to obtain local seeds, seeds were obtained from the Louisiana Forest Seed Company. The seeds for *C. canadensis* were placed in near boiling water and left to sit overnight before cold storage at 5ºC for seven days before planting to encourage germination (Louisiana Forest Seed Company, personal communication).

In spring 2006, a total of 2592 seeds were planted in 24, 1x1 m test plots. Each plot consisted of 54 *C. florida* seeds and 54 *C. canadensis* seeds. Hardware cloth was staked on top of the plots and one seed was planted per square. Seedling success of those that germinated was measured by counting the number of seedlings that were present in each plot once a month for 3 months (See Figure 4 for a design schematic). This design allowed the simultaneous testing of two experimental factors and their interaction (the effect of *M. vimineum* and the effect of light) on germination success and early survivial.

The presence and/or absence of *M. vimineum* was manipulated by hand removal of all herbaceous material within the study plot. The effects of light environment on germination were determined by placing plots either within blowdown areas (high light) or under a fully developed primary canopy (low light but not under a secondary canopy). A total of six pairs of plots were deployed in each of the high light and low light environments in this 2x2 factorial design. Significance of each factor as well as their interaction was determined by a two-factor ANOVA (SAS version 8.2; Ott and

Longnecker 2001) with light environment (blowdown or under canopy) and presence of *M. vimineum* (presence or absence) as the main factors.

Results

Seed Dispersal

Cornus florida seed production differed between 2006 to 2007 as determined by seed trap counts. Over 300% more seeds were collected in 2007 as compared to 2006. In 2006, 86 fully pulped, 11 partially eaten and 50 depulped seeds were collected. In 2007, 424 fully pulped, 65 partially eaten and 110 depupled seeds were collected. While in both 2006 and 2007 the York-James region of Virginia (where this study was conducted) experienced a moderate drought, 2006 was more severe with 70% less precipitation than normal from February 1st to April 8th compared to 2007 with 53% less precipitation than normal from March 1st to July 22nd (VDEQ 2006 and 2007). The reduced seed production in 2006 may have been caused by these drought conditions.

The size of the trees canopies at each trapping location ranged from 3-6m, which is consistent with what has been reported elsewhere (e.g., 3.8 -4.6 m. Gilman and Watson 1993). The average canopy extension from the trunk of tree 498 (the solitary tree) was 3.6 m. Tree 471 (middle of glade) had a canopy that extended 5.7 m, whereas the other tree in the glade, Tree 468, at the edge had a canopy extension of 3.05 m. As the canopies of these three trees are in or close to the normal ranges for *C. florida,* it was expected that

their seed distributions would behave as predicted by the JCEH (Jansen 1970, Clark *et al.* 1999).

The JCEH predicts that *C. florida* seeds would be dispersed away from the maternal individual with the majority of seeds dispersed proximate to the mother and an asymptotically decreasing number of them dispersed further away (e.g., a leptokurtic distribution). However, this was not always true depending on the year and seed type. To determine the shape of the distribution kurtosis was measured. A leptokurtic distribution, which has the majority of values around the mean has a positive kurtosis (Zar 1984). A negative kurtosis indicates a platykurtic distribution which has the majority of values between the mean and tails (Zar 1984). A normal distribution will have a kurtosis of zero. Table 1 displays the measure of kurtosis for each seed type each year. Tree 468 (located at the edge of a glade) and tree 498 (a solitary tree) both had more than 94% of seeds dispersed into traps located within 2.75 m of the tree each year. Tree 471 (located in the middle of the glade) had a relatively equal proportion of seeds dispersed into each trap located at 1.25m, 2.75m, 4.25m and 5.75m. No seeds were dispersed into traps beyond 5.75m at this trapping location. The seed counts in this trap may be biased by the other trees in the glade that most likely contributed seeds to these counts.

The percentage of seeds dispersed into each trap at each tree was fairly consistent between the two years and the three seed types (Figure 5). The average dispersal distance over the 2 years of seed trapping was 2.35 m (95% CI 2.26-2.45) from the tree for all three trapping sites (Figure 6). The average dispersal distance for tree 471, which was located in the middle of the glade, was 3.34 m (95% CI 3.15-3.52), the average dispersal distance for

tree 468, which was located at the edge of the glade, was 1.97 m (95% CI 1.88-2.07), and the average dispersal distance for tree 498, the solitary tree, was 1.59 m (95% CI 1.47-1.71; Figure 6). The mean dispersal distances estimated from each array were significantly different as their confidence intervals do not overlap.

Light Environments

The three light environments measured; open field, beneath a *C. florida* and the upper canopy, and beneath patches of *M. vimineum* just outside of a *C. florida* canopy (but still beneath the upper canopy), were statistically different using an ANOVA ($F=905.57$, $p<0.0001$, Table 2). The average PFD in the open field was 8.6 ± 0.5 $mol \cdot m^{-2} \cdot day^{-1}$, the average PFD under the *C. florida* canopy was 0.58 ± 0.33 $mol \cdot m^{-2} \cdot day^{-1}$, and the average PFD beneath a patch of *M. vimineum* was only 394 ± 414 $\mu mol \cdot m^{-2} \cdot day^{-1}$. A Post-hoc test showed that all three testing locations had mean light values that were significantly different from each other.

Using the average PFD in the open field to represent total ambient light, the *C. florida* canopy was found to reduce the local light environment to 6.7% of available light. Under the canopy of *M. vimineum* the amount of light was reduced to 0.005% of total available light.

The secondary canopy provided by *C. florida* also had a significant influence on the presence of the invasive, *M. vimineum.* A total of 285 *M. vimineum* individuals were sampled from 9 replicate plots located underneath the primary forest canopy (but devoid of a secondary canopy). Sample plots located underneath the additional secondary-canopy

created by *C. florida* individuals reduced the number of *M. vimineum* individuals by a third (N = 82). Across all replicates, the mean number of *M. vimineum* specimens was significantly smaller in the *C. florida* sub-canopy treatment (t=10.19, df=16, p<.0001, Figure 7). This result is consistent with past studies that show a decline in *M. vimineum* performance as canopy cover is increased (e.g., Cole and Weltzin 2005, Gibson *et al.* 2002.)

Recruitment

The recruitment of mid-canopy seeds was studied in four types of test plots in a 2x2 factorial design: (1) plots in blowdown areas that had not been cleared of *M. vimineum*, other herb species and litter, (2) plots in blowdown areas that had been cleared of all vegetation and litter, (3) plots beneath the upper canopy with the presence of leaf litter, and (4) plots beneath the upper canopy that had been cleared of leaf litter. The number of mid-canopy seeds germinated varied in each of these test plots (Figure 8). The largest amount of initial germinates were found in the plots that were located in blowdown area (high light) and had been cleared of all herbaceous plants (no *M. vimineum*). The smallest number of germinates were found in plots that were located beneath the over canopy (low light) and had not been cleared (*M. vimineum* present).

There was a significant difference in the mean number of initial *C. canadensis* germinates between plots that had been cleared and plots that had not been cleared (F=24.74, df=3, p<0.001). While there was a larger number of *C. florida* germinates in plots that had been cleared compared to plots that had not been cleared, there were too few

specimens to generate a significant result. Low overall recruitment for *C. florida* across all treatment combinations may have contributed to this result. These data were collected during June 2006, at which point the plots that had been cleared of all herbaceous vegetation and leaf litter had new *M. vimineum* germinates emerging with the *C. florida* and *C. canadensis* specimens.

By July 2006, the plots that had been cleared were hard to differentiate from the plots that had not been cleared, as the *M. vimineum* had densely grown back. There was a 65% decrease in the number or *C. canadensis* seedlings that were present from June to July in the plots that had originally been cleared and located in the blowdown area. In the uncleared plots within a blowdown area, the number of *C. canadensis* seedlings was reduced by 44% from June to July. In this same time period, the number of *C. canadensis* seedlings in blowdown plots that had been cleared had remained relatively constant, whereas *C. florida* seedling numbers continued to decline. This suggests that seedling success as well as germination success is affected by the presence of *M. vimineum*.

There appears to be a possible interaction between the canopy/blowdown area variables (Figure 9) and population size of germinates. However, the limited growth seen in the canopy areas is likely due to the pine-leaf litter located in these areas (Fike 1999). The pine stands could also create soil conditions that are not ideal for most seed germination and growth.

Discussion

The most important outcome from my results is that the area within which maximal recruitment may be possible can be significantly modified by the presence of invasive species. This is particularly important when one considers the time scales that influence dispersal and invasion. Mechanisms that influence dispersal distance in plants are both complicated and highly evolved traits that have been refined at an evolutionary timescale. By definition, the invasion of novel species into new habitats typically occur within a very short time, perhaps too short for resident species to respond to this changing competitive environment. From the perspective of the JCEH, the area within which optimal germination is expected is severely reduced and pushed closer to the parent individual.

The movement of seeds is the main determinate of the structure of plant populations and a significant factor in a plant's ability to reproduce. Knowing patterns of dispersal are important so that recruitment limitations can be assessed and environmental changes can be identified and either controlled or fixed (Clark *et al.* 1999). While *C. florida's* dispersal pattern seen in my study was not perfectly leptokurtic as Janzen-Connell predicted, the majority of seeds were dispersed well within the average extension of the *C. florida* canopy at each of the trapping locations. If the dispersal results from tree 471 (which may be skewed because of its location in the middle of the glade with several

potential seed parents contributing) are removed, most seed types had a positive kurtosis with the majority of seeds falling close to the parent plant.

Where and how a seed is dispersed can either be advantageous or detrimental to that seed's ability to grow and succeed. *Cornus florida* is mainly dispersed by birds and/or gravity. If a bird ingests a seed it will generally defecate it beneath another *C. florida* canopy or beneath a similarly fruiting tree (Clark *et al.* 2004). Kwit *et al.*(2004) found no increase in a *C. florida* seed's success when it was dispersed beneath a similarly fruiting tree. Thus, regardless of dispersal type, most seeds are dispersed into what the JCEH considers an unfavorable environment where seeds must face competition for resources with its stronger parent plant and a higher rate of predation due to the large volume of seeds dispersed in a relatively small area (Janzen, 1970).

Another hurdle that a seed must overcome is the presence of a dominant plant in the vicinity of where it was dispersed. Dominant herbaceous plants may monopolize nutrients, light, and ground space that a seedling would need to thrive. Tree seeds may face higher mortality rates because it takes longer for a seedling to grow beyond neighboring herbaceous plants competitive effects (Berkowitz *et al.* 1995). Invasive species may increase the severity of competition. By definition, invasive species must be able to colonize a new territory and replace existing flora. There are several different mechanisms that invasive species use to gain a competitive advantage during the process of invasion and subsequent persistence on-site

In the piedmont region of Virginia, where this study was conducted, patches of *M. vimineum* are surrounding adult *C. florida* trees. *Microstegium vimineum* creates a light

environment that can make seed germination and success difficult. Beneath patches of *M. vimineum* light is reduced 99.995% when compared to ambient light. Both *C. florida* and *C. canadensis* are considered to be shade tolerant trees that are able to successfully recruit under a fully developed upper canopy. However, there is a minimum threshold of light that is required for both of these secondary canopy species to germinate and survive during the first year of growth. The recruitment results from this study offer evidence that the occurrence of *M. vimineum* has a negative effect on germination and seedling success in several ways. First, numbers of initial germinates were significantly lower in plots that had not been cleared of *M. vimineum* (compared to plots that had been cleared). Seeds require moisture, a suitable temperature and the presence of oxygen to germinate. Often, if seeds are dormant, they will also require a "priming" treatment such as a specific amount of light or fluctuating temperature to trigger germination (Bewley and Black 1994). *Microstegium vimineum* may affect the germination of seeds like *C. florida* and *C. canadensis* by altering one of the germination requirements. For example, if *M. vimineum* becomes too dense it may block water from reaching the soil layer where a seed may be located, thus depriving seeds of the moisture needed for germination. Also, if a seed requires light stimulus to come out of dormancy *M. vimineum* may prevent the threshold light level from reaching the seed by having such a dense cover.

Next, the seed bank of *M. vimineum* quickly established a new population of individuals in the sites where all herbaceous vegetation was removed. This had a detrimental effect on the number of mid-canopy seedling that were able to persist in the presence of the invasive grass. This suggests that as fewer numbers of mid-canopy trees

are able to survive in locations where *M. vimineum* has invaded, the mid-canopy population structure will become unstable. What is unclear at this point is the extent to which species other than *M. vimineum* may influence recruitment. It is possible that both *C. florida* and *C. canadensis* seedlings are particularly poor competitors during early establishment independent of who their competition. Given the presence of both species on site and the lack of any surviving *C. florida* and *C. canadensis* individuals in the treatments that had *M. vimineum*, my data suggests that *M. vimineum* is a more effective competitor than the existing set of herbaceous species with which these trees typically interact.

While the germination results support my hypothesis, the fact that very few seeds were able to germinate in the plots located beneath the upper canopy outside of the blowdown areas raises a few questions. The minimal growth seen in these canopy areas is probably due to the pine-leaf litter, which produces soil conditions that are not optimum for seed germination (Fike 1999). The next step in this investigation would be to run a similarly designed experiment while replicating it in a greenhouse with synthetically produced canopy cover. This would ensure that soil type and other variables that were not controlled in this experiment remain constant. If different light environments were simulated, an ideal range of light needed for *C. canadensis* and *C. florida* seed germination could be found. This would add more support to the argument that the presence of *M. vimineum* is detrimental to mid-canopy seed success. Another experiment that this work suggests would be following seedling success for both *M. vimineum* and mid-canopy seeds over several years. This would first show if *M. vimineum* is able to adapt to the lower light

conditions beneath mid-canopy plants. It would also help to quantify the rate of reduction of mid-canopy trees. This would allow long-term predictions to be made about the fate of deciduous forests. Moreover, following tree recruitment success over several years will provide more accurate estimates of overall recruitment than during a single year.

Microstegium vimineum's spread at the Rice Center is very expansive. At present, its occurrence will make it difficult for any *C. florida* seeds to germinate and thrive if they are dispersed into it. However, noticeable gaps in *M. vimineum* are present beneath *C. florida* canopies at the Rice Center. The results of this study showed a significant reduction in the amount of *M. vimineum* beneath *C. florida* secondary canopies compared to areas only covered by an upper canopy. The amount of light that penetrates beneath a *C. florida* canopy may be the major deterrent of *M. vimineum* growth and spread. Combining these light penetration results and the predictions of the JCEH leads to an assumption that in the presence of *M. vimineum*, the ideal place for seed recruitment would be at the outside edge of a parent canopy. This would provide protection from the spread of *M. vimineum* while keeping the seed farther from the parent plant. The size of the JCEH "doughnut" is dictated by the size of the spatiotemporal variation surrounding the parent canopy (Nathan *et al.* 2000). Situations where *M. vimineum* has invaded may cause a paradigm shift in terms of the size and location of the JCEH's "doughnut".

My results combined with those from Cole and Weltzin's 2005 study suggest that *M. vimineum's* plasticity, dense growth pattern and persistent seed bank may be an 'invasive multiplier'. This term represents characteristics of an invasive species that accentuate its invasive ability to not only take over a habitat that is ideal for the seed

success of native plants, but to also prevent the growth of, in this case, trees that can inhibit its growth. As *M. vimineum* is not regularly present under mid-canopy trees such as *Juniperus virginiana, Asimina triloba* (Cole and Weltzin 2005) and *C. florida,* it can be hypothesized that most other mid-canopy trees would have a similar effect on *M. vimineum*. So, *C. florida* and other mid-canopy trees can be considered a form of natural control for *M. vimineum*. These findings suggest that the presence of an understory invasive grass can significantly influence the recruitment and future competitive ability of the mid-canopy tree community in deciduous forests. A smaller JCEH "doughnut" will lead to fewer mid-canopy trees being recruited. Also, as the Janzen-Connell "doughnut" is reduced it would become closer to the parent tree. Over time, this would cause mid-canopy trees to become clumped together at much finer spatial scales than they currently are. As the mid-canopy plants clump together, larger, high-light habitats will allow plants that are more tolerant to the sun to take over. This may lead to effects on native fauna that require the presence of the mid-canopy layer for optimum light environments, for particular nesting needs or for a food source.

These results give implications for a drastically changed forest landscape in the future. I predict that as the current generation of mid-canopy trees dies off, there will be fewer mid-canopy trees to replace them, and eventually the result will be clumped mid-canopy trees. Projecting out even further in time we may see a complete loss or extinction of the understory.

David Quammen wrote an article in Harper's Magazine in October 1998 discussing extinction. He predicted that the Earth is heading towards another mass extinction and

detailed the casual factors as well as forecasted what the world would look like after the extinction. One of the main drivers he named was invasive species or "weeds" and suggested that as species move to new locations, ecosystems may be tremendously changed. He also eloquently predicted that "forests will be tiny insular patches existing on bare sufferance, much of their biological diversity (the big predators, the migratory birds, the shy creatures that can't tolerate the edges, and many other species linked inextricably with those) long since decayed away. They'll essentially be tall woody gardens, not forests in the richer sense…Earth will be a different sort of place – soon, in just five or six human generations. [His] label for that place, that time, that apparently unavoidable prospect, is the Planet of Weeds." This study suggests that as *M. vimineum* may be causing a reduction of the mid-canopy, the resulting effects on the overstory need to be examined. First, the relationship between *M. vimineum* and upper canopy seed germination and seedling success needs to be established. Then, the overall effects of the absence of a sub-canopy on the overstory need to be studied. We would hypothesize that maintaining an expansive and strong mid-canopy layer, which may serve to help control *M. vimineum,* would be important in maintaining the current forest structure and may help to prevent the Earth from turning into a "Planet of Weeds" (Quammen 1998).

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APPENDIX A

Tables

Table 1. Kurtosis of seed dispersal curve for the three trees from which seeds were collected in 2006 and 2007.

	Seed Type	Fully pulped		Partially Eaten		Depulped	
	Year	*2006*	*2007*	*2006*	*2007*	*2006*	*2007*
Tree	**498**	5.99	2.93	-1.88	3.66	5.98	5.08
	468	-1.88	-1.39	6	-1.81	6	-2.14
	471	5.56	-1.03	1.43	3.14	5.39	-0.04

Table 2. ANOVA table with the F-statistic and p-value for the three light environments measured, open field, beneath *C. florida* and beneath *M. vimineum.*

Source	**df**	**MS**	**F**	**p**
Model	2	29945254548	905.57	<0.0001
Error	16	33067773		
Corrected Total	18			

APPENDIX B

Figures

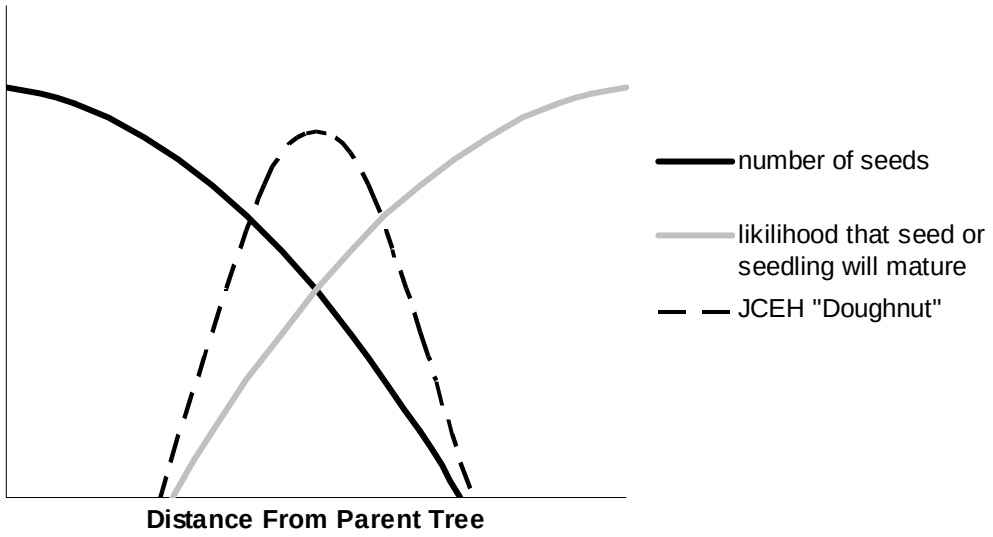
number of seeds
likilihood that seed or seedling will mature
JCEH "Doughnut"
Distance From Parent Tree

Figure 1.

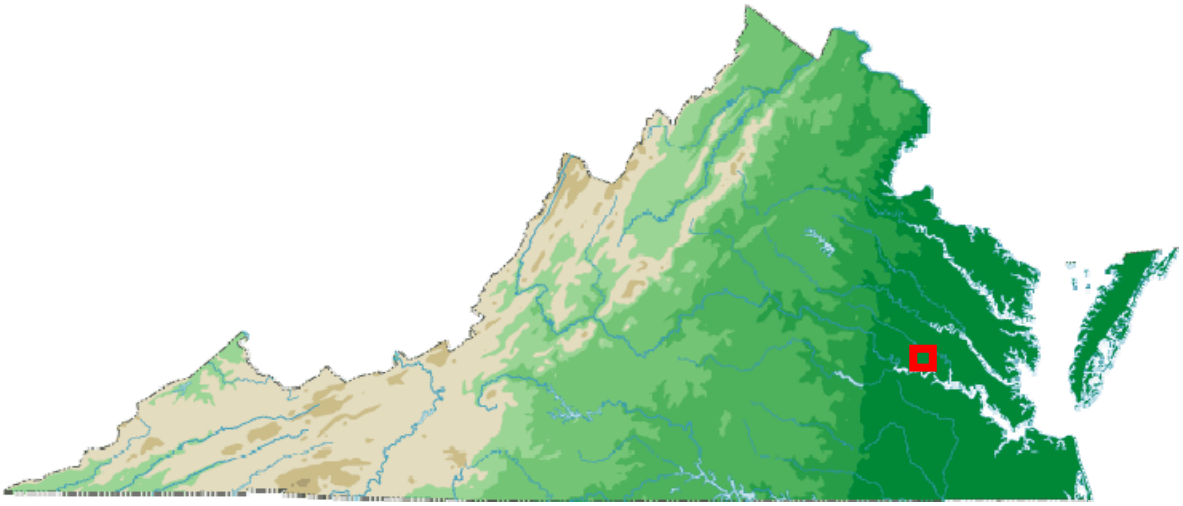

Figure 2. Virginia-Map.org

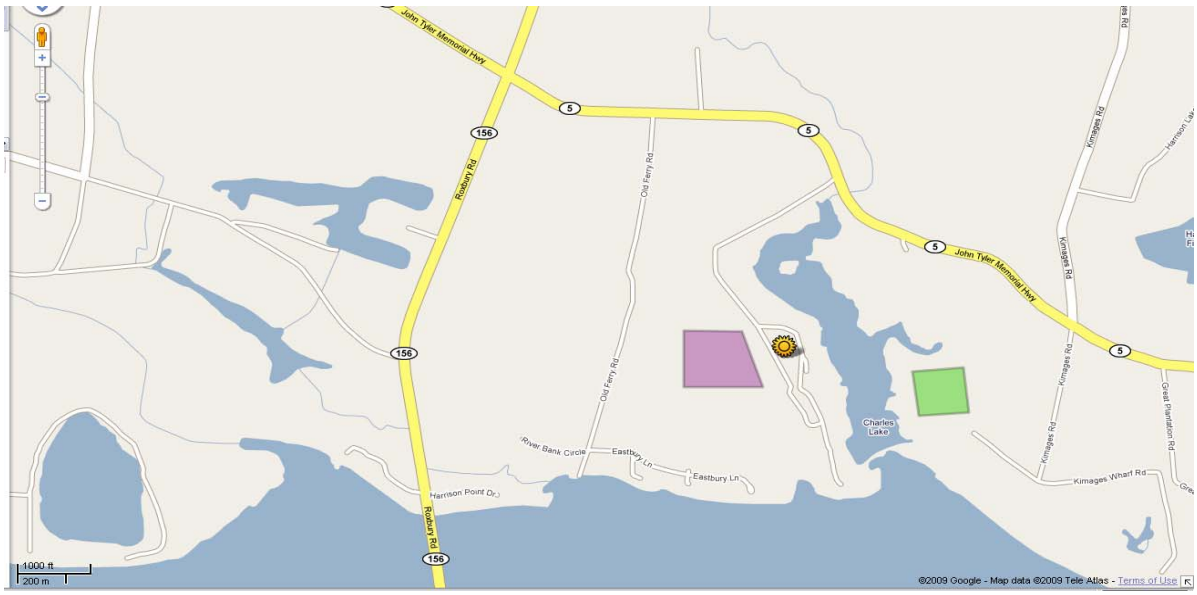

Figure 3.

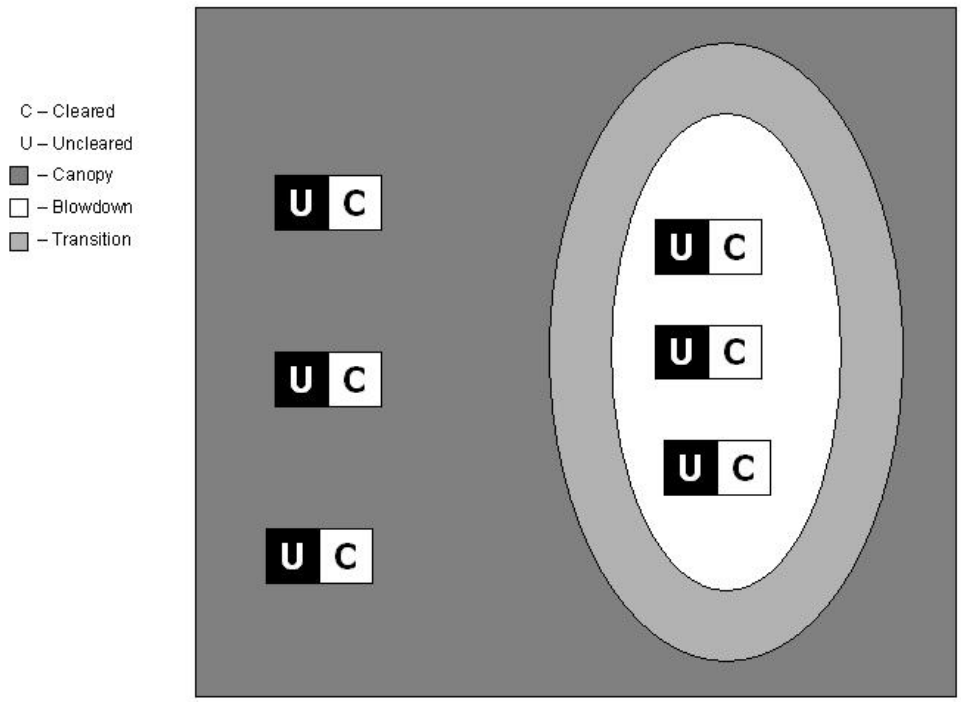
C – Cleared
U – Uncleared
– Canopy
– Blowdown
– Transition
U C
U C
U C
U C
U C
U C

Figure 4.

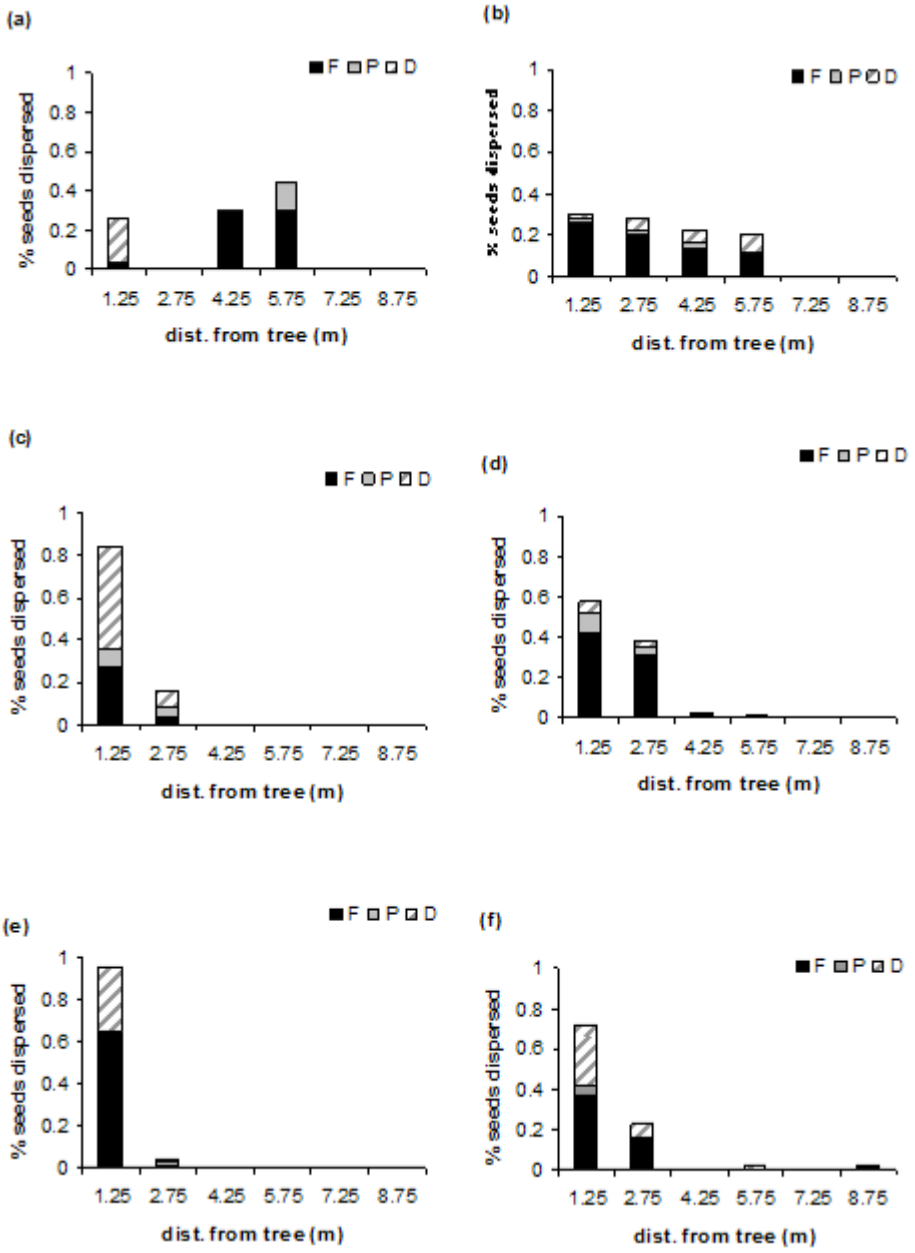
(a)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)
(b)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)
(c)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)
(d)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)
(e)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)
(f)
F P D
% seeds dispersed
1
0.8
0.6
0.4
0.2
0
1.25 2.75 4.25 5.75 7.25 8.75
dist. from tree (m)

Figure 5.

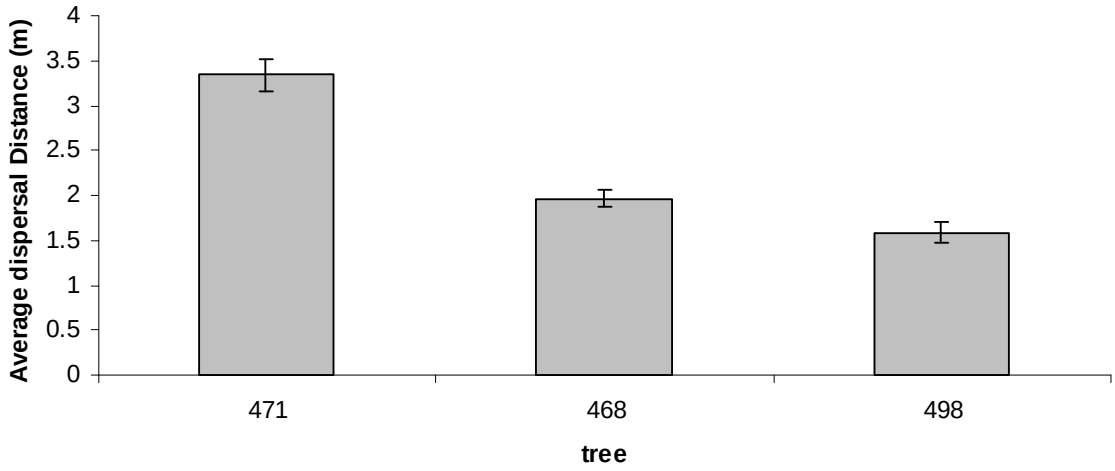

Figure 6.

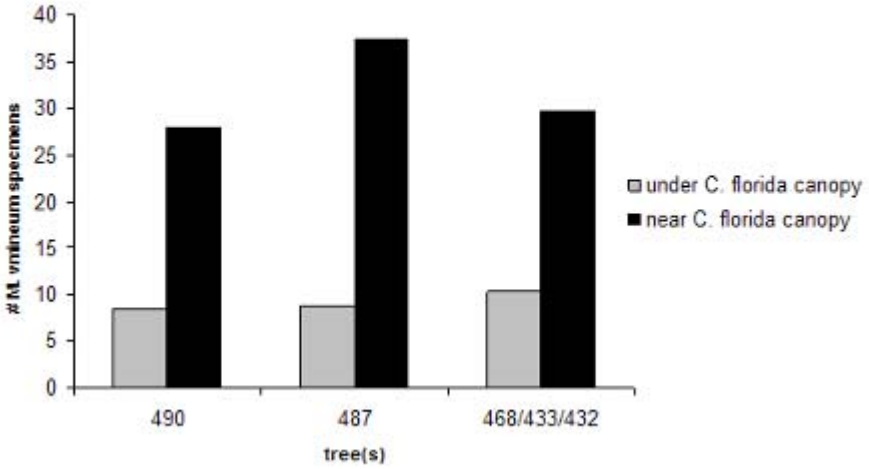

Figure 7.

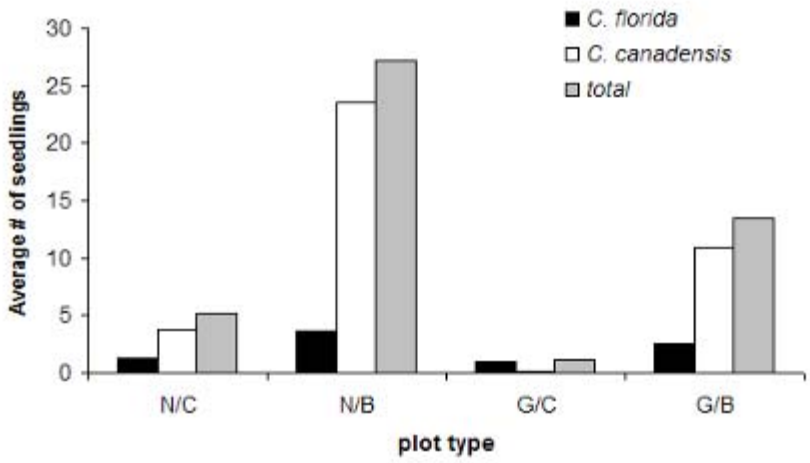
C. florida
C. canadensis
total
Average # of seedlings
30
25
20
15
10
5
0
N/C
N/B
G/C
G/B
plot type

Figure 8.

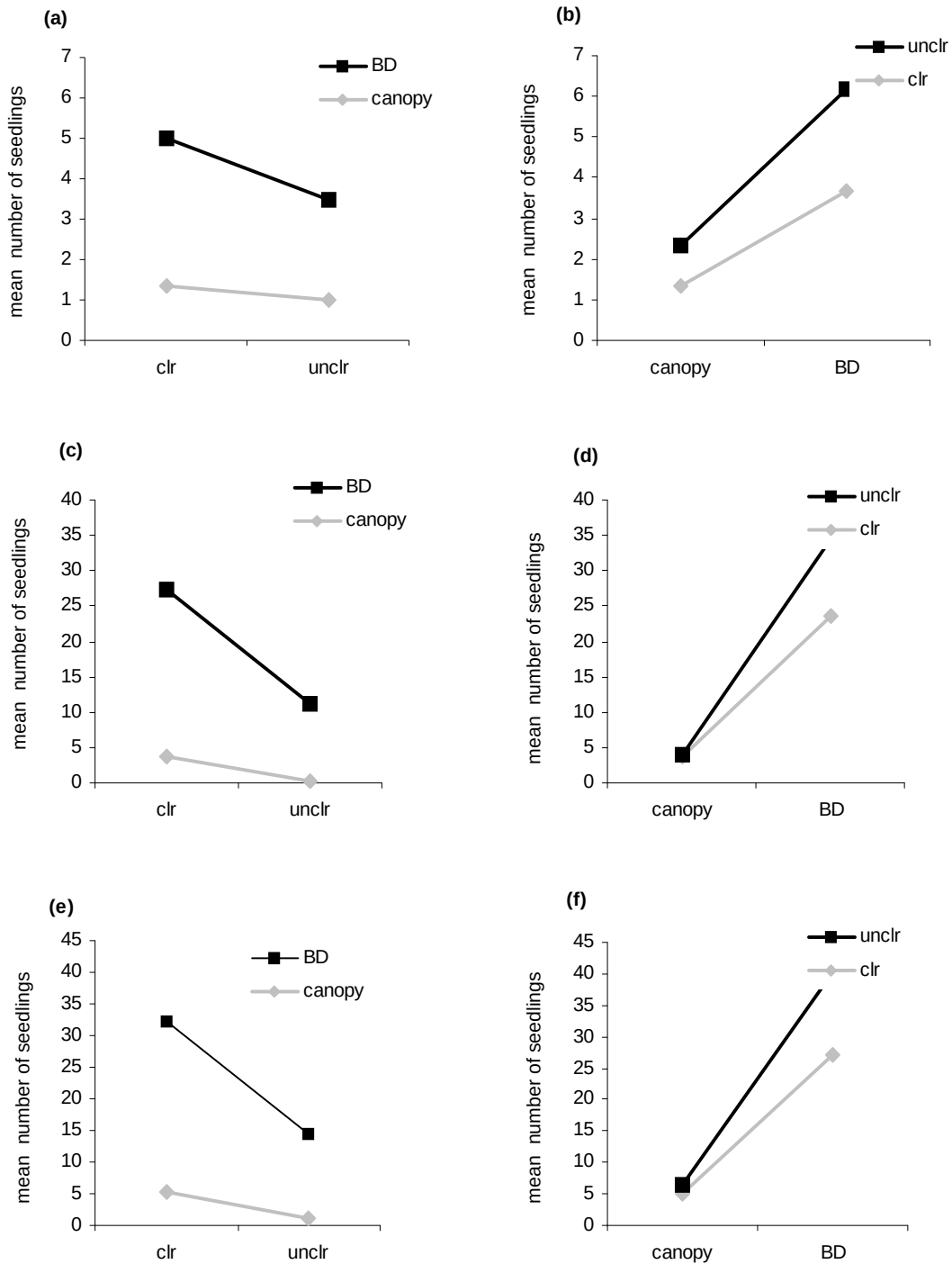
(a)
mean number of seedlings
BD
canopy
clr
unclr
(b)
mean number of seedlings
unclr
clr
canopy
BD
(c)
mean number of seedlings
BD
canopy
clr
unclr
(d)
mean number of seedlings
unclr
clr
canopy
BD
(e)
mean number of seedlings
BD
canopy
clr
unclr
(f)
mean number of seedlings
unclr
clr
canopy
BD

Figure 9.

VITA

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